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THE HOMOLOGIES OF THE FINS OF FISHES.

BY E. D. COPE.

I. THE RELATION OF FINS TO LEGS.

ALTHOUGH it is well established that the paired fins of fishes are, as a whole, homologous with the limbs of the higher vertebrates, and although many naturalists have given their views upon the homologies of the respective parts, the subject is yet involved in considerable doubt; and, as stated by Prof. Huxley in 1871, the basal and radial supports of the fins themselves can only be identified in the most general way with the limb-bones or cartilages of other vertebrata.

The doctrine that the vertebrate limbs are modified ribs was advocated, to a varying extent and with modifications, by Maclise[1] (1832) and Oken[2] (1843); while Owen[3] (1848) regarded them as diverging appendages attached to ribs, with a shoulder-girdle of axial origin. Professor Goodsir[4] (1857) considered the limbs as homologous with the epipleural spines of fishes, and external to the proper visceral wall of the body. Professor Humphrey[5] (1871) concluded that the vertical fins were of bifold origin, since the dorsal and ventral mid-lines of the body are formed by the junction of the bifold *laminæ dorsales* and *ventrales.* He considered that the pectorals and ventrals were certain portions of the lower azygos fins, prevented from uniting by the interposed body-cavity. Maclise had previously regarded the distal portions of the limbs as corresponding with the azygos fins. In 1876 Balfour[6] described the development of the limbs of Elasmobranchs as "special developments of a continuous ridge on each side, precisely like the ridges of epiblast which form the rudiments of the unpaired fins," and concludes from this "that the limbs are remnants of continuous lateral fins." The primitive folds persist in the vertical and caudal fins, while the paired fins represent portions of such folds (Fig. 1).

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[1] Todd's Encyclopædia, Vol. IV., p. 70. Fig. 490.

[2] Lehrbuch der Natur-Philosophie, p. 330.

[3] Archetype and Homologies of the Vertebrate Skeleton.

[4] *Edinburgh New Philosophical Journal*, Vol. V., 1857, p. 178.

[5] *Cambridge Journal of Anat. and Physiol.*, Vol. V. (Second Series, Vol IV.), p. 58, Plate II.

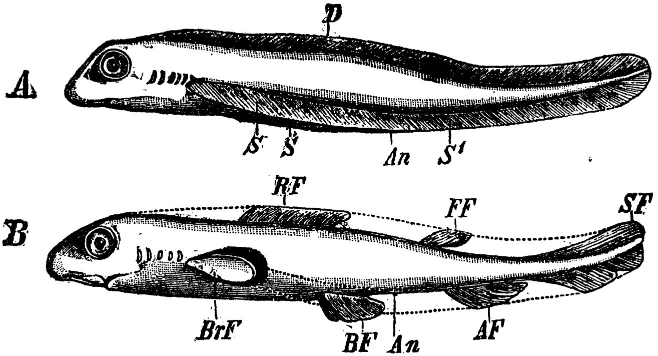

FIG. 1.—Diagrammatic representation of primitive and derivative types of lateral and median fins. *A*, primative condition, fins continuous; *B*, derivative condition, fins distinct and specialized; *D*, dorsal fins; *Br F*, pectoral; *B F*, ventral: *A F*, anal; *S F*, caudal; *R F*, dorsal; *F F*, second dorsal fin; from Wiedersheim.

As regards their intimate structure, those of the Elasmobranchs and Polypterus occupy in some sort a middle term between those of the Teleostomata and those of the Dipnoi. In order, therefore, to trace out the homologies between the segments of the paired fins of the Teleostomata and those of the limbs of the Reptilia, the parts must be traced in lineal order through the following classes or sub-classes: Reptilia, Batrachia, Dipnoi, Elasmobranchii, Teleostomata. (Figs. 2, 3.) Naturalists disagree in the interpretation of the homologies of these parts, but if the view enunciated by Balfour of the origin and development of the paired limbs is the correct one, it is possible that a homology can be traced along the downward scale of limb-development from the Batrachia on the one hand, and the Teleostomata on the other, to the ancestral type of the Ichthyotomi of the Carboniferous, the oldest limb type known.

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[6] Ibid., Vol. XI., Part I., p. 132.

Dr. Gill[7] traces out the relationship of the members of the shoulder-girdle in the Dipnoi with those of the Batrachia as follows: The proximal element of the anterior limb of the Dipnoan is the homologue of the humerus. In the Urodela the humerus is articulated chiefly with the coracoid; therefore, the element of the Dipnoan shoulder-girdle with which the humerus is articulated is the coracoid, unless evidence to the contrary can be produced. The scapula in the Batrachia is entirely or almost excluded from the glenoid foramen, therefore the corresponding element in the Dipnoi must be the scapula. The element of the Dipnoan shoulder-girdle continuous downwards from the scapula, and to which the coracoid is closely applied, is named by Gill the ectocoracoid. Each half of the shouldergirdle is surmounted by an element which is named the supraclavicle by Gegenbaur, the suprascapula by Gunther, the scapula by Owen; and this is in turn connected with the skull by another element, the posttemporal of Parker and Gill, who justly observe that there is an *à priori* improbability against the homology with the scapula of any part having a ligamentary connection with the humerus-bearing element.

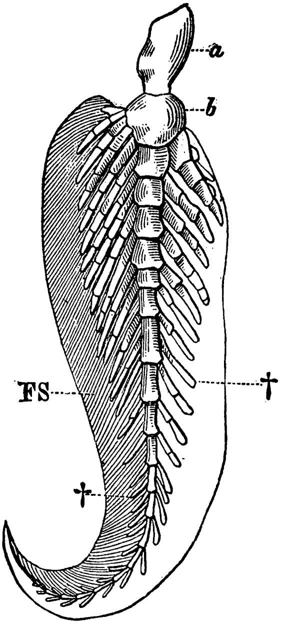

FIG. 2.—*Neoceratodus forsterii*, pectoral, fins, unibasal type; *a b*, axial elements; †, radials; *F S*, fin-rays; from Wiedersheim.

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[7] Arrangement of the Families of Fishes, Nov., 1872. Smithsonian Misc. Col., Vol. XI.

As far as his argument applies to the Dipnoan pectoral Gill, may be safely followed, except in his view of the element abutting upon the occiput, which he regards as having intimate relations with the skull, and probably originating from it. In tracing back the homologies of the parts of the Dipnoan to those of the teleostome shoulder-girdle, Dr. Gill is less cogent, and the nomenclature adopted by Gegenbaur[8] appears preferable. The latter author figures the right half of the shoulder-girdle and the thoracic fin of a teleostome fish (Gadus). Here there is no humerus

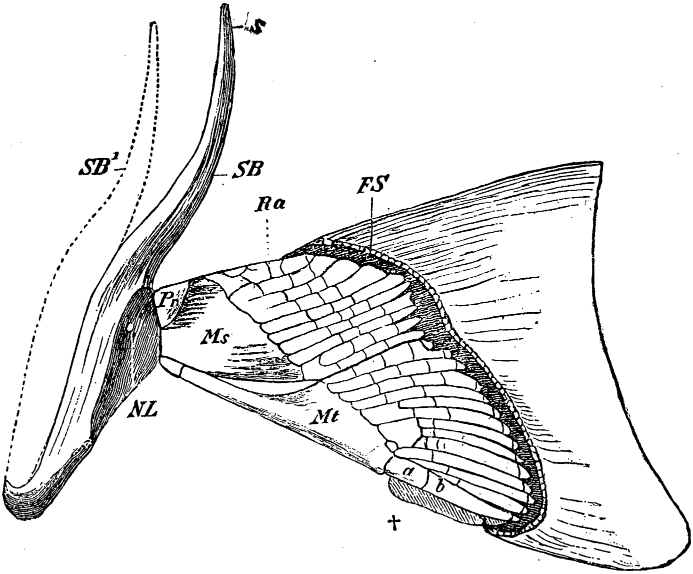

FIG. 3.—*Heptanchus griseus*, left pectoral fin, pluribasal type. *SB*, scapular arch; *NL*, foramen; *Pr*, propterygium; *Ms*, mesopterygium; *Mt*, metapterygium; *a b*, exis of metapterygium; *Ra*, basilars; *FS*, fin-rays; from Wiedersheim.

recognizable as such, but that the so-called "carpals" or basilars of the fin are regarded as representing it, is evident from the fact that the bone to which they are attached is styled the coracoid, and that which abuts against it the scapula. The element corresponding to the "proscapula" of Gill, and formed, according to him, of the united scapula and ectocoracoid, is by Gegenbaur called the clavicle, which is attached to the supraclavicle above. The bone connected with the skull is, as has been said before, named the posttemporal by Parker. The clavicle of Gegenbaur is the coracoid of Owen,[9] while his scapula is Owen's ulna, and his coracoid the radius. As Gill remarks, Owen first sought to determine an ulna and radius, and then identified the other bones from their relations to it. (Figs. 3 and 4.)

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[8] Elements of Comparative Anatomy, Second Edition, p. 475, 1877.

But, even though the terms used by Gegenbaur be adopted as representing most nearly the correspondences between the parts of the shoulder-girdle of the Dipnoi and Stapedifera on the one hand, and those of the Teleostomata, Crossopterygia, Podopterygia, and Elasmobranchs on the other, an exact homology is not yet positively assured. Hence Gill has subsequently termed Gegenbaur's scapula hypercoracoid, and his coracoid the hyopocoracoid.

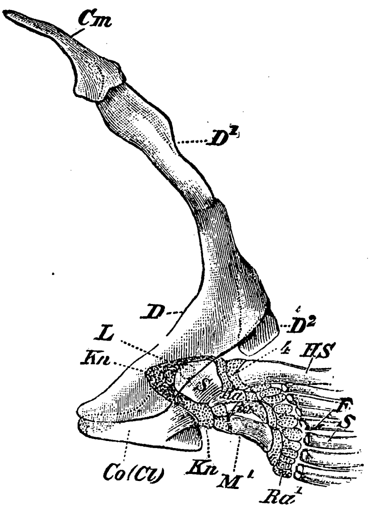

FIG 4.—*Salmo fario*, left shoulder-girdle; *Cm*, posttemporal; D^1, epiclavicle; *D*, clavicle; D^2, postclavicle; *S*, scapula; *Co*(*Cl*), coracoid; *Ra*, basilars; *L*, scapular foramen; *HS*, *FS*, fin-rays.

In the ventral fins the process of concrescence is carried to a considerable extent in Polypterus and the Chrondrostei, and farther still in Amia, Lepidosteus and the Teleostomata, which agree in the possession of a single large elongated element proximal to the basilars in each ventral. To this base are attached four long basilar rays in Polypterus, nine in *Accipenser brevirostrum*, and three minute ossicles in the Teleostomata. The elongated supporting bone is styled by Thacher a pubis, and Wiedersheim has recently shown that it is a part of the pelvis, and, being preacetabular, is the homologue of the pubis.[10] The conclusion that can be arrived at from a study of both the pectoral and ventral fins is that the limbs of all air-breathing mammals or Stapedifera (possessed of a stapes) form a group more nearly related to each other than any of them are to any other vertebrate groups; and that the archipterygian form is to be found in the unibasal pectoral and ventral fins of the Ichthyotomi, the unibasal Crossopterygia, and the Dipnoi. (Plate XIV.)

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[9] Comp. Anat. and Physiol. of Vertebrates, Vol. I., p. 106.

[10] *Anatomischer Anzeiger*, 1889, IV.

These are substantially the conclusions arrived at by Mr. Thacher,[11] who names the group composed of the Dipnoi and higher vertebrates the Choanata, from their possession of "choanæ," or posterior nares opening behind the lips. But the Ichthyotomi and the unibasal Crossopterygia were not known to him.

According to Gegenbaur,[13] the archipterygium, or primitive form of limb from which all the limbs of the Gnathostomes, or vertebrates with lower jaws, have been developed, is to be found in its parent form in the limb of Ceratodus, which consists of an elongated, tapering, many-jointed rod, bearing upon each side a series of rays. In a previous paper,[14] the fin of Protopterus, bearing on the outer side only a series of rays, had been taken as the type. In the second edition of his "Grundriss," Gegenbaur adheres to the idea enunciated in his later article,[15] and identifies the metapterygium of Acanthias and other Elasmobranchs, plus one only out of the many rays, with the main stem of the fin of Ceratodus; while the propterygium, mesopterygium, and all the other rays of the Elasmobranch fin are regarded as developments from the lateral rays of a Ceratodus-like fin. By a further slipping off of the rays from the main- or stem-row, Gegenbaur derives the many-rayed fins of the Teleostomata from those of the Elasmobranchii, which he has previously asserted to be derived

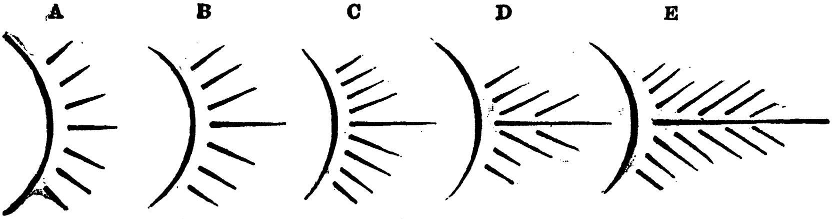

FIG. 5.—Archipterygium *E*, and transitional stages to actinopterygium *A*, according to Gegenbaur; from Wiedersheim.

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[11] Ventral Fins of Ganoids. Trans. Conn. Acad., IV., 1877, p. 242.

[13] Anatomy of Vertebrated Animals, p. 36.

[14] *Jena. Zeitschrift*, Bd. VII., Hft. 2, pp. 131-141.

[15] Ibid., Bd. V., Hft., 4.

from those of the Dipnoi. Huxley,[16] in 1876, concurred in this view of the archipterygium, but regarded the main stem as passing through the fifth finger instead of through the thumb, an arrangement which Gegenbaur has adopted in his second edition. (Fig. 4.)

As has been shown, the view propounded by Mr. Thacher in 1877,[17] and also independently worked out by Prof. Balfour, namely, that the paired fins of all vertebrates are formed from a continuous lateral fold, corresponding to the median fold from which the vertical fins of fishes are derived, is that which is supported by the greater weight of evidence, and is now most generally adopted. It is strongly supported by the extinct genus of Acanthodean fishes, Climatius, in which a series of spines extends on each side of the abdomen from the pectoral to the ventral fins. And these spines are said to be similar to those which support the anterior border of these fins. The evidence of paleontology is, however, equally in favor of the unibasal paired fin (archipterygium) as the ancestral form, as it characterized the oldest Elasmobranchii (Ichthyotomi) and Crossopterygia, while the pluribasal type is of later age in both divisions of fishes. But it may have been derived from a continuous fin, as suggested by Climatius.

If this view be followed, the Dipnoan paired fins must be regarded as a derivative from the paired fins of the Ichthyotomi, which must still be looked upon as the form from which the limbs of the Stapedifera or air-breathing vertebrates have been derived. Baur believes that the latter have been constructed from a simple axis like that of Lepidosiren by a process of budding, and not by rearrangement of the branches of a fin of the Ceratodus type. The Teleostomata, although specialized in many ways, stand on one side of the upward line that leads to the reptiles, birds, and mammals, and their paired fins retain much of the primitive character.

2. THE RELATIONS OF FINS TO EACH OTHER.

The paired limbs of the higher vertebrates appear, at first sight, exceedingly unlike the fins of fishes, yet it has long been believed by naturalists that the pectoral and ventral fins of the latter are the homologues respectively of the fore and hind limbs of the former. But between the paired fins of fishes and the median or vertical fins there are also resemblances which warrant a suspicion of their origin from similar primitive structures, nsomuch that it is now believed by many that the median fins are derivatives from a primitive continuous vertical fold, while the paired fins are the specialized remainders of primitively continuous lateral folds.

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[16] Proc. Zoöl. Soc. Lon., 1876, Pt. 1, on *Ceratodus forsterii.*

[17] Proc. Conn. Acad., Vol. II., p. 281.

Cope, writing in 1870,[18] remarks upon the analogy that exists, on the one hand, between the succession in the type of the pectoral fin, commencing with the simple axis of the Dipnoi, and passing to the axis with lateral appendages or radii, seen in Selache, and, on the other hand, the succession by which the median fins of Polypterus pass from rays with a jointed, forked extremity continuous with the base (in the caudal part of the series) to the structure that obtains in the dorsal pinnules, which consist of a strong spinous ray from the posterior face of which a number of soft rays project. He also regarded the segments which support the dorsal and anal rays in ancient fishes and Elasmobranchs as homologous with those which support the rays of the pectoral and ventral fins, and calls them all basilars, and, in a later essay, [19] baseosts. He showed that the baseosts experience the same reduction with time in all the fins, being obliterated in the dorsal, anal, and ventral fins in nearly all modern Teleostomata, and being reduced to four or fewer in the pectoral fin in most of the same.

A most carefully worked out contribution to this portion of the developmental history of vertebrate appendages is that of J. K. Thacher,[20] who converts the analogy noticed by Cope into a homodynamism, and regards the Dipnoan paired fins, not as maintained by Gegenbaur,[21] as the primitive form or archiptery-

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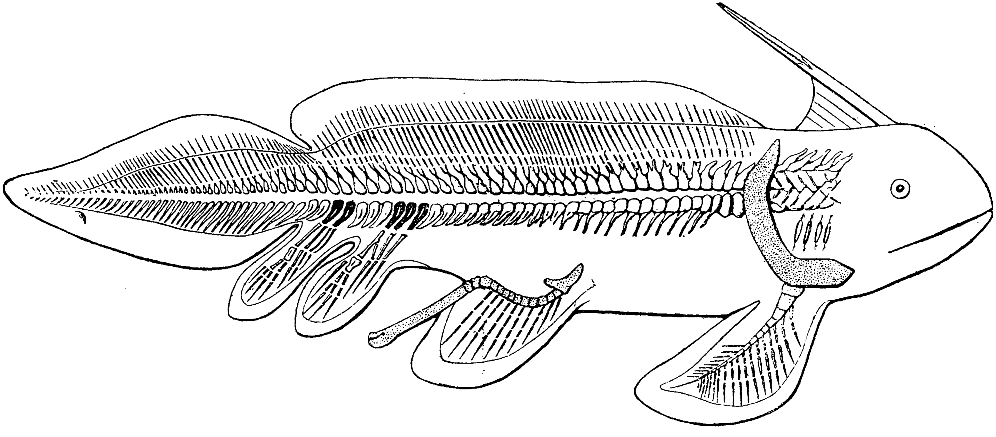
[18] Contribution to the Ichthyology of the Lesser Antilles. Amer. Philos. Society, XIV., 446-483, 1870.

[19] AMERICAN NATURALIST, 1887, p. 1016.

[20] Median and Paired Fins. Trans. Conn. Acad., Vol. III., 1877.

[21] *Jena. Zeitschrift*, Bd. V., Hft. 4. Gegenbaur über den Gliedmaassen der Wirbelthiere im Allgemeinen und der Hintergleidmaassen der Selachier in besonders. May, 1870.

PLATE XIV.



Xenacanthus decheni.

gium, but as a derivative from the primitive series of parallel rays of the lateral folds.

The conclusions of this writer respecting the median fins are as follows: The primordial median fin-rays are derived from a series of parallel chondroid rods, which grow up in the median fold totally independent of the cartilaginous arches above and below the notochord. The earliest representatives of these parts, as the quadrate markings at the base of the median fin in Branchiostoma, and the fin-rays of Myxine and Petromyzon, are much more numerous than the vertebræ opposite them. Therefore, neither are median fin-rays derived from neural spines, nor neural spines from primordial fin-rays, but neural spines are formed by the dorsad prolongation and union of the neurapophyses of the vertebræ.

This statement, which is supported by the structure, not only of the lower fishes mentioned above, but that of the Elasmobranchs, which have from 2 to 3.5 fin-rays to one vertebra, and that of Acipenser, is in opposition to the earlier opinion of Gegenbaur,[22] who asserts that the primordial fin-rays, in their simplest form, are mere prolongations of the neural spines.

The primitive fishes have been shown by Cope to sustain the view of Gegenbaur. The invariable equality of number between the vertebræ and the actinophores (see section 3, below) in Dipnoi is supposed by Thacher to be the result of the entire loss of the primordial median fin-rays, the long and segmented supports of the median fold in Lepidosiren, Ceratodus, etc., being simply elongated neural spines. This view is not sustained by paleontology.

Carrying his argument onwards to the lateral or paired fins, Mr. Thacher shows that the ventral and dorsal fins of *Mustelus canis* agree in every respect save the separateness of the basal elements in the latter, and their coalescence in the former, and argues that this certain amount of similarity warrants us in inferring an earlier state when the similarity was greater. The similarity between the structure of the anal and ventral fins of Acipenser is evident from an inspection of the figures. The theory put forward by Thacher, is, therefore, as follows: As the dorsal and anal fins

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[22] Grundriss der Vergleichenden Anatomie, 1873, p. 488.

were specializations of the median folds of Branchiostoma, so the paired fins were specializations of the two lateral folds which are the homologues of the Wolffian ridges, in embryos of higher forms. Rods formed in both median and lateral folds. In the latter, these became at least twice segmented, the orad ones were prolonged inwards, more or less concresence took place, and the cartilages spreading, met below in the middle line, and later, extending dorsad, completed the limb girdle. Gegenbaur, in the later edition of his "Grundriss," has modified his views respecting the nature of the primordial fin-rays, since he says:[23] "Supporting organs, formed from the integument, are connected with the parts thus formed by the vertebral column (superior and inferior arches), and they are continued into the caudal fin. In the Selachii the fin-rays are formed by the so-called horny filaments, and in the Ganoidei and Teleostei by ossifications."

The same eminent anatomist, who has aided so greatly in establishing the relationship between the various parts of the simple paired fins of the Dipnoi, and those of the air-breathing vertebrates (Stapedifera, Thacher), refuses to concede the homodynamism of the median and paired fins, but adheres in the later edition of the "Grundriss" to the theory propounded by him in 1872,[24] namely: their derivation from the branchial arches, by the articulation of the simple lateral rays set upon those arches to the central ray, which gradually assumes increased length, and becomes an axis. In this way a fin like that of Ceratodus might be produced.

The views of Mr. Thacher are, however, supported by the independent but later observations of Balfour,[25] who found that in the embryo dogfish the lateral fins have precisely the same mode of origin as the dorsal median fin, arising "as special developments of a continuous ridge on each side, precisely like the ridges of epiblast which form the rudiments of the unpaired fins."

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[23] Elements of Comparative Anatomy, by Carl Gegenbaur, 1877. (Translated by F. Jeffrey Bell, B.A., 1878), p. 431.

[24] Untersuchungen zur Vorgleichenden Anat. der Wirb., Hft. III., Kopfskelet der Selachier, p. 181, Note, 1872.

[25] Balfour. Development of Elasmobranch Fishes, 1878.

A later contribution to this branch of the subject is contained in a paper entitled "Notes on the Fins of Elasmobranchs, with considerations on the Nature and Homologues of Vertebrate Limbs," by St. George Mivart, published in the Transactions of the Zoölogical Society of London, February, 1879. After noting and discussing the opinions of Oken, Carus, Cuvier, Owen, Gegenbaur, Balfour, Parker, and others, upon this and other questions relating to the history of vertebrate appendages, the author states his conviction "that the nature of the paired and azygos limbs is fundamentally the same." This conviction was formed through finding various degrees of coalescence between the cartilaginous rays supporting the dorsal fins, and various degrees of connection or continuity between such fin-supports and the axial skeleton. *Scyllium canicula*, *Ginglymostoma cirratum*, and still more *Notidanus cinereus*, are examples of this. In the latter, the rays are supported by one continuous basal cartilage. Pristis and Pristiophorus show continuity between the dorsal fin-cartilages and the skeleton, and this may aid in the support of the saw-like rostrum. In Notidanus, Chiloscyllium, and Raia, there is much resemblance between the skeleton of the ventral and dorsal, in Notidanus, between the ventral and anal, while the ventrals of Polyodon are simple parallel rays like the simplest form of the dorsal skeleton. If the ventrals are thus admitted to be of the same nature with the vertical fins, the pectorals must also be of the same nature.

Prof. Mivart endorses the idea of Mr. Thacher with regard to the origin of the limb-girdles, viz.: that they are lateral ingrowths from the skeleton of the paired fins. The objection to this conclusion that has been drawn from the attachment of the pectorals by a shoulder-girdle instead of by direct longitudinal adhesion are met by the considerations that such adhesion would impede the flexure of the body in swimming, that the pectorals are too low to abut directly on the vertebral column, and that such connection is prevented by the intermediation of the body-cavity. The entire theory is thus summarized by Mivart:

1. Two continuous lateral longitudinal folds were developed similar to a dorsal and a ventral fold.

2. Separate, narrow, solid supports, with their long axes di-

rected outwards, were developed to a varying extent along the lines of these folds.

3. The longitudinal folds were interrupted variously, leaving two prominences on each of the lateral folds.

4. The anterior prominences (or limbs) increased more than the posterior.

5. The bases of the cartilaginous supports coalesced according to the needs of the various isolated parts or fins.

6. Occasionally the dorsal radials coalesced, and sought centripetal adhesion to the axis.

7. More constantly the hinder laterals coalesced, and finally prolonged themselves inwards by mesiad growths till such a pelvic structure as is found in Squatina was developed.

8. The pectoral rays also coalesced proximally, and, in search of a support, shot dorsad and ventrad to avoid the visceral cavity. They thus attained the axis above and came together below.

9. The lateral fins, as they were used for support, became elongated and segmented, till probably the propterygium, but possibly the mesopterygium, became the axis of the digit-bearing limb.

10. Pre-existing cartilages were enlarged, or new ones were developed, at the distal ends of the paired limbs, till the cheiropterygium (leg) was developed.

11. The pelvic limb acquired a solid connection with the spine from the need of a firm support on land.

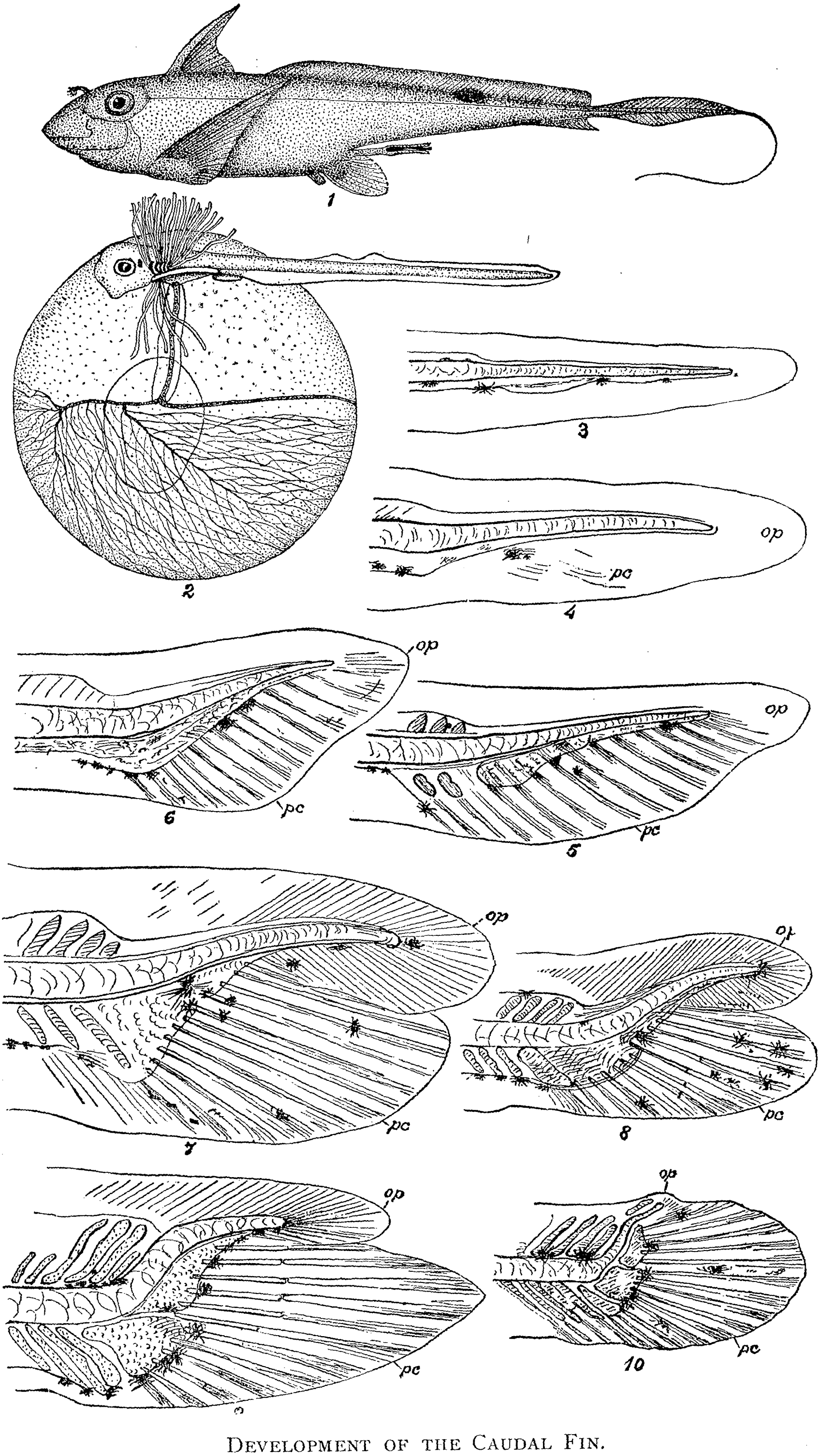
12. The pelvic limb became elongated.

These changes all came about from external causes acting on the plastic animal organism, and the limitation of the paired limbs to four was determined solely by locomotive convenience.

Prof. Mivart gives Mr. Thacher the credit of the first promulgation of the ideas he has adopted, but does not follow the latter in his conclusion that median fin-rays are never derived from neural spines, nor neural spines from fin-rays, as he considers this point to be unsettled, and only capable of proof by the study of their development.

The discovery of the structure of the pectoral and ventral fins in the Ichthyotomi by Sauvage and Döderlein, has substantiated

PLATE XV.



Development of the Caudal Fin.

the view of Huxley that the fins of Ceratodus represent the archipterygium or primitive paired fin, as distinguished from a primitive lateral continuous fin, which the theory of Balfour leads us to anticipate may be yet discovered, and which is partly realized in the extinct genus Climatius. And whatever homology may be traced between the paired and median fins, it is evident that the axis of the former has undergone changes which the latter have not experienced. This consists in the sliding proximad of some of the lateral branches of the axis, so that there came to be two, three, or more axial pieces attached to the point of support or scapula. The primitive type is termed by Huxley unibasal, and the later type pluribasal. In the Elasmobranchii the paired fins are unibasal in the Ichthyotomi, and pluribasal in the Selachii. In the Holocephali all are pluribasal. In the Dipnoi the known forms are unibasal. In the Crossopterygia the majority are unibasal, but the order of Cladistia (Polypteridæ) are pluribasal, having two or three (as they are counted) axial bones articulating with the scapula. In other Teleostomata the paired fins are pluribasal, and have mostly lost the axial elements, the basilars only remaining (Fig. 4).

In any case the connection of the paired fins has not been traced to the vertebral axis, as is the case with the median fins, the scapular and pelvic arches being their support in the earliest stages and oldest types known. This has been completely established by the recent researches of Wiedersheim,[26] as far as embryology alone can do it.

As the case at present stands, whatever of proof morphology or embryology furnishes, is in favor of the similar origin and homology of the vertical and paired appendages, but that their relations with the skeletal axis are not identical.

3. ON THE NATURE OF THE SUPPORTS OF THE MEDIAN FINS.

In my memoir on the Fishes of the Lesser Antilles of 1870,[27] as already remarked, I have called attention to the systematic significance of the connection of the fin radii with the vertebral

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[26] *Anatomischer Anzeiger*, 1889, No. 4.

[27] Transactions of the American Philosophical Society, p. 450.

column through the intermediation of the supporting elements in certain cases. In a review of Zittel's Paleontology of Fishes, published in 1887,[28] I applied the facts of this part of the structure to the question of taxonomy and phylogeny more fully, establishing the subclass Rhipidopterygia, and several orders, on the varying characters of the median fin supports. Some additions were made to this system in a "Synopsis of the Families of the Vertebrata," published in 1890.[29] The basis of this analysis is the hypothesis above cited, that the fins represent longitudinal folds of the integument, within which have been developed rods which form a framework connecting the free edges of the folds with the vertebral column. These rods may have been primitively undivided neural spines, but in the oldest forms known to us two segments exist distad to the neural spine. These I have termed the axial and basal elements, or the axonost and the baseost; the latter supporting the fin-rays when they exist. Fin-

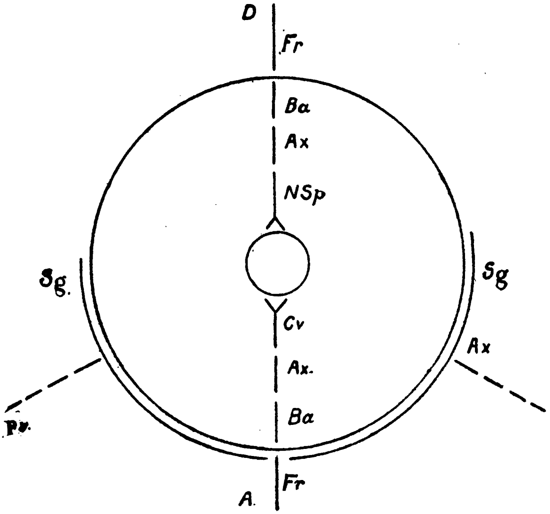

FIG. 6—Diagram representing the elementary constitution of the fins; *D*, dorsal fin; *A*, anal fin; *Pv*, pectoral and ventral fins; *NSp*, neural spine; *Ax*, axonost; *Ba*, baseost; *Fr*, fin-ray; *Cv*, chevron bone; *Sg*, shoulder girdle.

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[28] AMERICAN NATURALIST, 1887, p. 1016.

[29] AMERICAN NATURALIST, 1889, October, published March, 1890.

rays, however, have developed as a result of specialization of less important and more delicate hair-like bodies, described by previous authors, which traverse the fin from base to border within, and which Prof. Ryder has called actinotrichia, and which he says originate in the mesoderm.

I have determined that continuity of neural spine, axonost and baseost is characteristic of all primitive fishes; while these are again to be distinguished into types which preserve the primitive actinotrichia, and those in which fin-rays are developed. In the latter case the fin-rays are always continuous with the baseosts or axonosts. (Fig. 7.) It has been long known that in modern fishes the axonosts have severed their connections with the neural spines, and do not correspond with them in number or position. The axonosts are then termed interneural and interhæmal bones. It is also a character of modern fishes (most Teleostomata) that the basilar bones are rudimental or wanting. The gradations between the primitive and modern types of fins represent the evolution of the class of fishes, and I have endeavored to express this view in the system which I have proposed, as above cited. (Am. Nat., October, 1889.)

The various stages or types of dorsal and anal fin structure may be defined as follows; and it seems necessary to give them names, to avoid the circumlocution requisite to express the characters in any other way. The diagrams appended explain the types referred to. They are applicable to the dorsal fin, and, inverted, to the anal fin. Each separate series in its totality is called by Ryder the actinophore. Its kinds are the following:

I. Actinotrichia present.	
Neural spine, axonost and baseost continuous;	*Entotetramerous.*
II. Fin-rays present.	
All the elements present and continuous;	*Ectetramerous.*
All the elements present, the axonosts not anticulated with the neural spines;	*Ectrimerous.*
Like the last, but the baseosts rudimental or wanting;	*Ecdimerous.*
Axonosts not connected with the neural spines, reduced to one or two for each fin;	*Rhipidopterygian.*

As I have already pointed out, there are two types of the Rhipidopterygian fin, the Rhipidistious where baseosts are present (teste, Traquair), and the Actinistious (Fig. 8) where they are wanting. These divisions, corresponding to orders, do not require renaming.

No fishes are known with the actinophore dislocated from the neural spines, and retaining actinotrichia. Should such be discovered, they will appropriately receive names similar to those given to the series with fin-rays, with the prefix ento, as entotrimerous, entodimerous, etc. For obvious reasons the discovery of an entotrimerous fish is more probable than that of an entodimerous one.

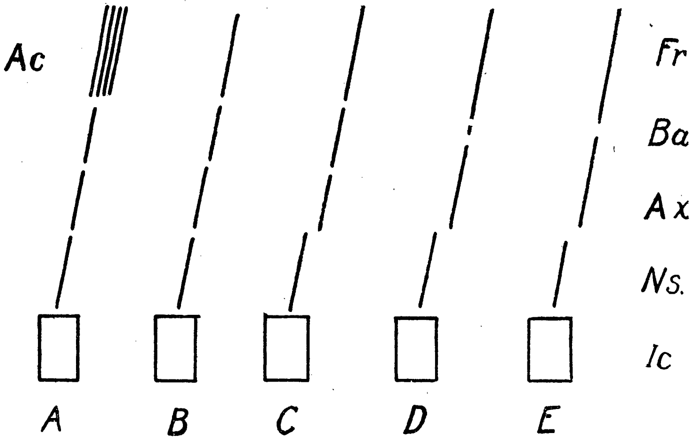
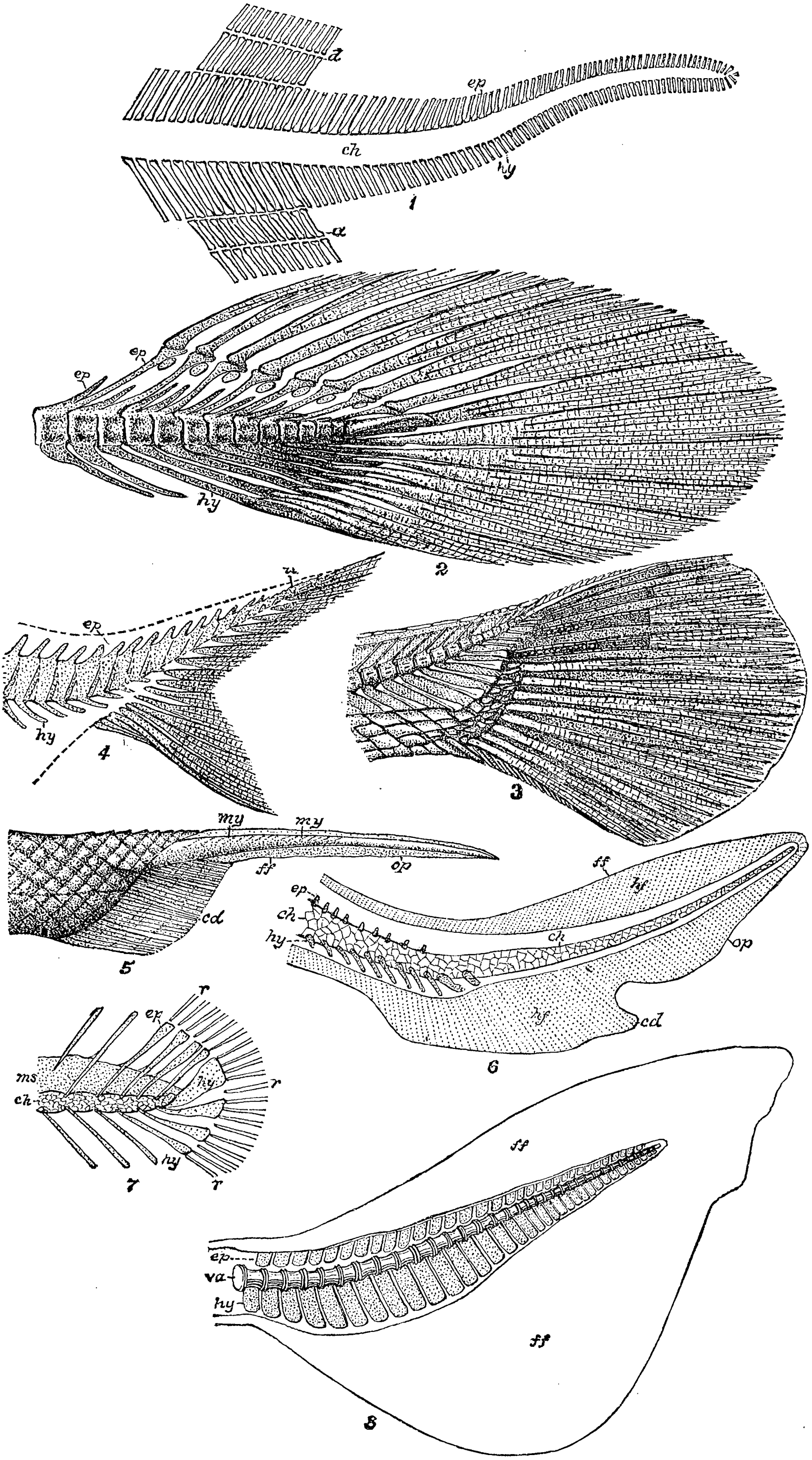


FIG. 7.—Diagrams of actinophores; *A*, entotetramerous; *B*, ectetramerous; *C*, ectrimerous; *D* and *E*, ecdimerous; *Ac*, actinotrichlia; *Fr*, fin-rays; *Ba*, basiost; *Ax*, axonost; *Ic*, intercentrum.

As regards the origin of the actinophores, Gegenbaur suggests that they were derived by segmentation from neural spines, while Thacher believes that they originated independently of the latter. Thacher bases his views on the structure found to exist in Selachii, which he supposes to represent the most primitive condition. The Selachii must, however, be regarded as, in many respects, degenerate, and Xenacanthus is probably more primitive. It is proba-

PLATE XVI.



DIPHYCERCAL AND HETEROCERCAL CAUDAL FINS.

ble however that Thacher's opinion is correct, but not for the reasons which he gives. I have oberved in a memoir On the Mechanical Origin of the Hind Parts of the Mammalia,[30] that "the mechanical cause of the origin of neurals pines may be traced to the strains upon the vertebral axis caused by a primary dorsal fold, or fin." [30] On this view the actinophores and the neural spines were simultaneously developed in lines of strain which naturally extend to the point of resistance nearest to the moving fin-fold, viz.: the apex of the neurapophysis. The development of the segments neural spine, axonost, and baseost was then simultaneous, and the one segment was not derived from the other. Thus the views of both Gegenbaur and Thacher are partially justified.

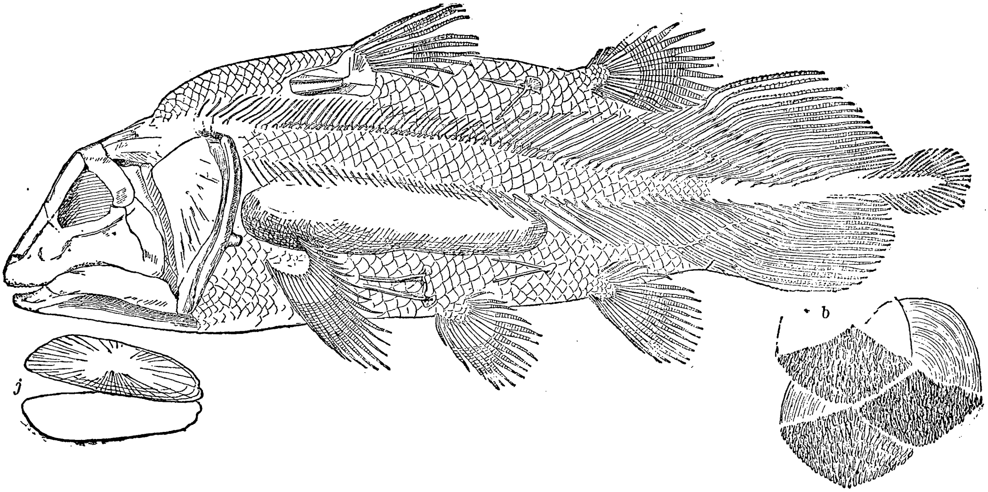


FIG. 8.—*Undina penicillata*, one-third natural size, showing rhipidopterygian and actinistious types of fins; *j*, jugular plates; *b*, scales of *Undina acutidens*; from Zittel.

The development of the appendicular skeleton is now shown to have proceeded from without inwards, and thus the homologies of the parts of the actinophores of all the fins must be interpreted from the same point of view, *i. e.*, from without inwards.

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[30] *American Journal of Morphology*, 1889, p. 210.

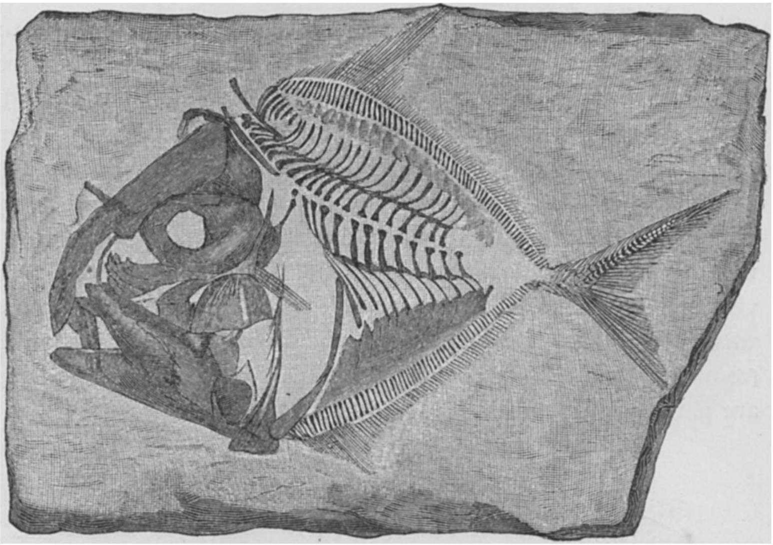

FIG. 9.—*Dorypterus althausii*, $\frac{1}{1}$. representing the order Docopteri, an actinopterygian fish from the Trias, with well developed baseosts of the median fins, and axonosts apparently continuous with the neural spines; from Zittel.

4. ON THE CAUDAL FIN AND ITS SUPPORTS.

Professor Louis Agassiz first called attention to the diversities in the structures of the caudal fins of fishes, and their relation to the general history of the class. He showed that the tails of modern fishes are constructed on two different patterns, which he called the homocercal and the heterocercal. In the former, the radial portion of the fin is in two unequal lobes, the superior being the more produced distally, and the inferior occupying a position on its inferior aspect, and having a much less degree of posterior prolongation. In the latter, the inferior lobe is of equal length and posterior prolongation with the superior. He showed that the homocercal type is characteristic of all Paleozoic and most of the Mesozoic fishes known to him, while the heterocercal type predominates in the Cenozoic and existing fishes. He also showed by a study of the embryology of the trout and other forms, that in their earlier stages the heterocercal fishes are homocercal. These results he regarded as important, and, in fact, they constituted the first intelligent application of the structural characters of fishes' fins to their systematic arrangement, which was made.

Subsequently the paleontologist McCoy,[31] observed that in some extinct fishes the vertebral column did not enter the superior part of the caudal fin, but continued directly to its middle base, and terminated without modification, the rods supporting the fin radiating equally and symmetrically above and below to the extremity. This type of fin he called diphycercal.

Later, Huxley[32] studied the development of the caudal fin in the salmon, and showed that although the caudal fin proper is heterocercal, some of the terminal vertebræ enter the base of the superior lobe, thus having a partially heterocercal structure.

Cope, in 1871,[33] reviewed the structure of the caudal fins of recent and extinct fishes. He stated that the diphycercal type (which he termed isocercal in ignorance of McCoy's paper) is the primitive condition of this region, preceding the homocercal in embryonic history. He showed that it persists in various modern fishes, as in the Lepidosiren and Polypterus, and among Telestomata, in the eel-like types, in the Gymnarchidæ, and in the Anacanthini, and in the last-named supporting a heterocercal caudal fin. He also showed that in various living isospondylous fishes besides the salmon, a partially homocercal condition persists, notably in the Notopteridæ.

A valuable contribution to this subject is that of E. T. Newton,[34] who has worked out some of the developmental stages of the sprat, and brings together the works of several earlier writers upon the subject. No notice is taken in this pamphlet of the writings of Cope, Wilder, and other American naturalists who have at various times observed or reasoned out the steps by which the primitive vertical fold becomes a highly differentiated caudal fin.

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[31] *Annals Magaz. Nat. Hist.*, 1848, p. 304.

[32] *Quarterly Journal Microscop. Science*, 1859, p. 33.

[33] Transactions of the American Philosophical Society, XIV., 1870, pp. 452, 453.

[34] On Fishes' Tails, by E. T. Newton, F.G.S. Ext. from the *Journal of the Queckett Microscopical Club*, July, 1882.

Ryder has given a very full account of the embryology of fishes' fins, which has especial reference to the caudal region.[35] He distinguishes six stages in the development of the caudal fin as follows:

1. Archicercy; no caudal fin-folds. 2. Lophocercy; caudal fin folds, with or without actinotrichia. 3. Diphycercy; 4, Heterocercy; and 5, Homocercy, as above defined. 6. Gephyrocercy, in which the terminal vertebræ are aborted, so that a hiatus is created between the neural and hæmal elements, or actinophores, at the extremity of the axis. This structure occurs in Echiodon (Pl. XVIII., Fig. 3,) Mola, etc. In this case the epaxial and hypaxial tegumentary folds are continuous round the extremity of the vertebral axis, and develop fin-rays which appear later than those of the dorsal and anal fins. This is supposed to be a condition of degeneracy.

The subject is treated histologically and embryologically by Ryder, who reviews the work of various authors who have viewed it from the same standpoint, especially Vogt, Kölliker, Dohrn, and Lotz.

The latest contribution to the subject is one by Baur, who shows that the rods (axonosts) which connect the rays of the anal fin with the inferior side of the caudal vertebræ, in Lepidosteus, are chevron bones.[36] This agrees with the determination by Cope[37] that the vertebral bodies of fishes are intercentra, and not centra.

From the researches already cited it is now well understood that in the caudal fin as in other fins, the primitive actinotrichia have become specialized into fin-rays, and that these approximate more nearly to the number of their osseous supports than do the actinotrichia. They are rarely so reduced in number, however, as to correspond exactly to the hypural bones.

The actinophores of the caudal fin may or may not have been primitively divided like those of the other median fins into

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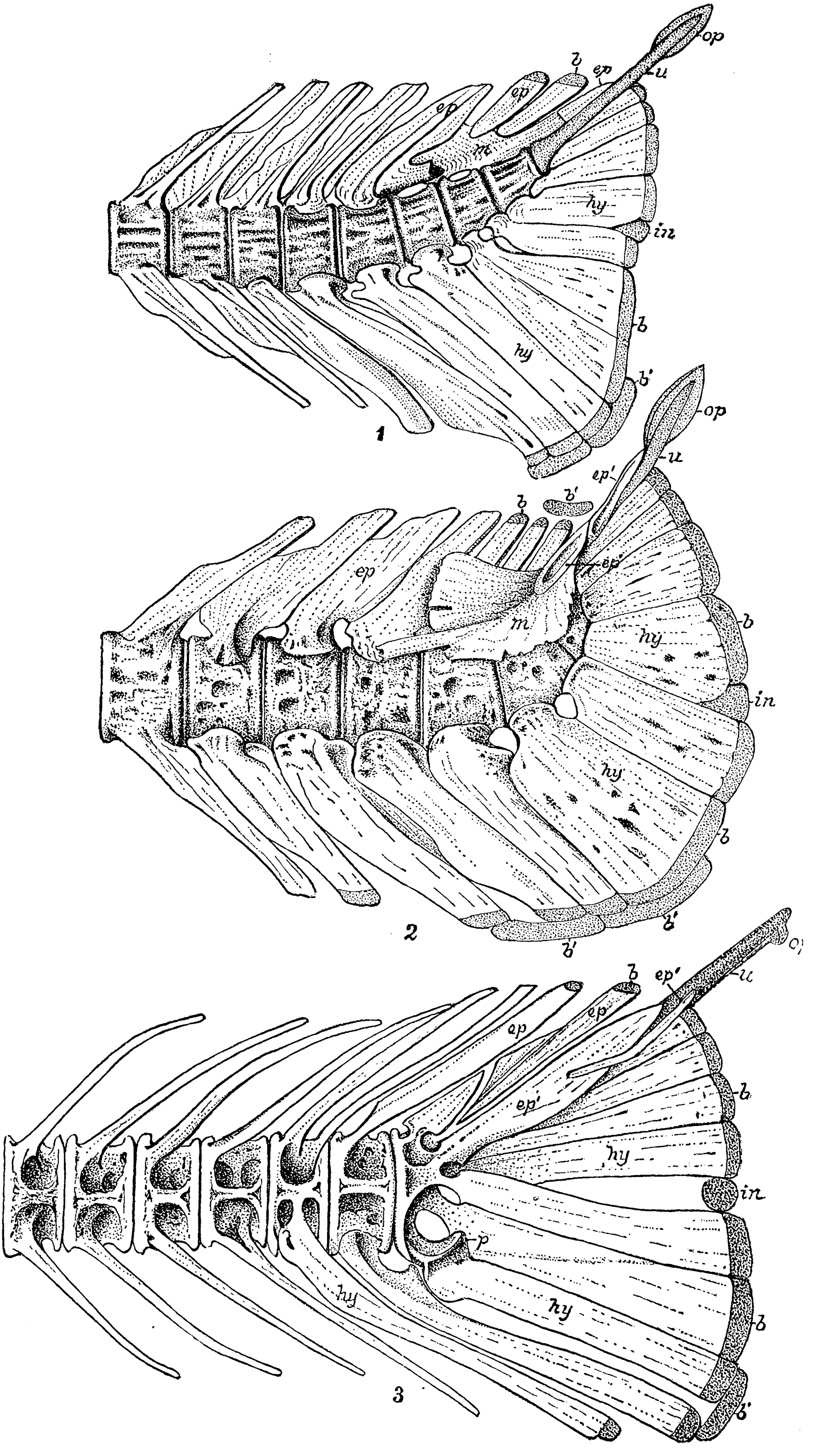
[35] Annual Report of the U. S. Commissioner of Fishes and Fisheries, 1886, pp. 981-1086.

[36] *Amer. Journal of Morphology*, 1889, p. 463. Dr. Baur inadvertently calls the axonosts "actinosts."

[37] Transac. Amer. Philosoph. Society, 1886, p. 243.

PLATE XVII.



Homocercal Caudal Fins.

(chevron) axonost and baseost. Such appears to have been the case with the Dipnoi, but whether it is strictly the case in the primitive Xenacanthus remains to be ascertained. The axonost and baseost are lost from the modern types of diphycercal tails, as Anguilla (Ryder, Pl. IV., Fig. 4) and Gadus.

The change from diphycercy to heterocercy is seen in the upward curvature of the extremity of the vertebral column, and the development of a portion of the inferior fin (anal) into a posteriorly projecting angle. This is the state of affairs in the Elasmobranchii, Chondrostei, and various extinct Teleostomata.

The change from heterocercy to homocercy is seen in the increased recurvature of the column, and the successive abortion of its extremity. This is accompanied by the increase in antero-posterior diameter of the hypural bones, especially distally, since they develop to occupy the space gained by the recurvature. The neural spines corresponding to them become correspondingly reduced. Such modified elements have been called (provisionally) hypural bones. All stages of development of these bones may be formed in the Teleostomata. Thus in the lower forms (most Malacopterygia) they remain distinct from each other. In many of the Acanthopterygia—e. g., Cottus, (Pl. XVIII., Fig. 1,) and Pharyngognathi, they are fused together, forming a continuous fan-shaped body, which supports the fin-rays directly.

The different types of hypural bones are well illustrated in the accompanying plates from Ryder.

EXPLANATION OF THE PLATES.

For the Plates XV. to XVIII., which are taken from those illustrating Professor J. A. Ryder's memoir on "The Origin of Heterocercy," I am indebted to the Hon. Marshall MacDonald, U. S. Commissioner of Fish and Fisheries.

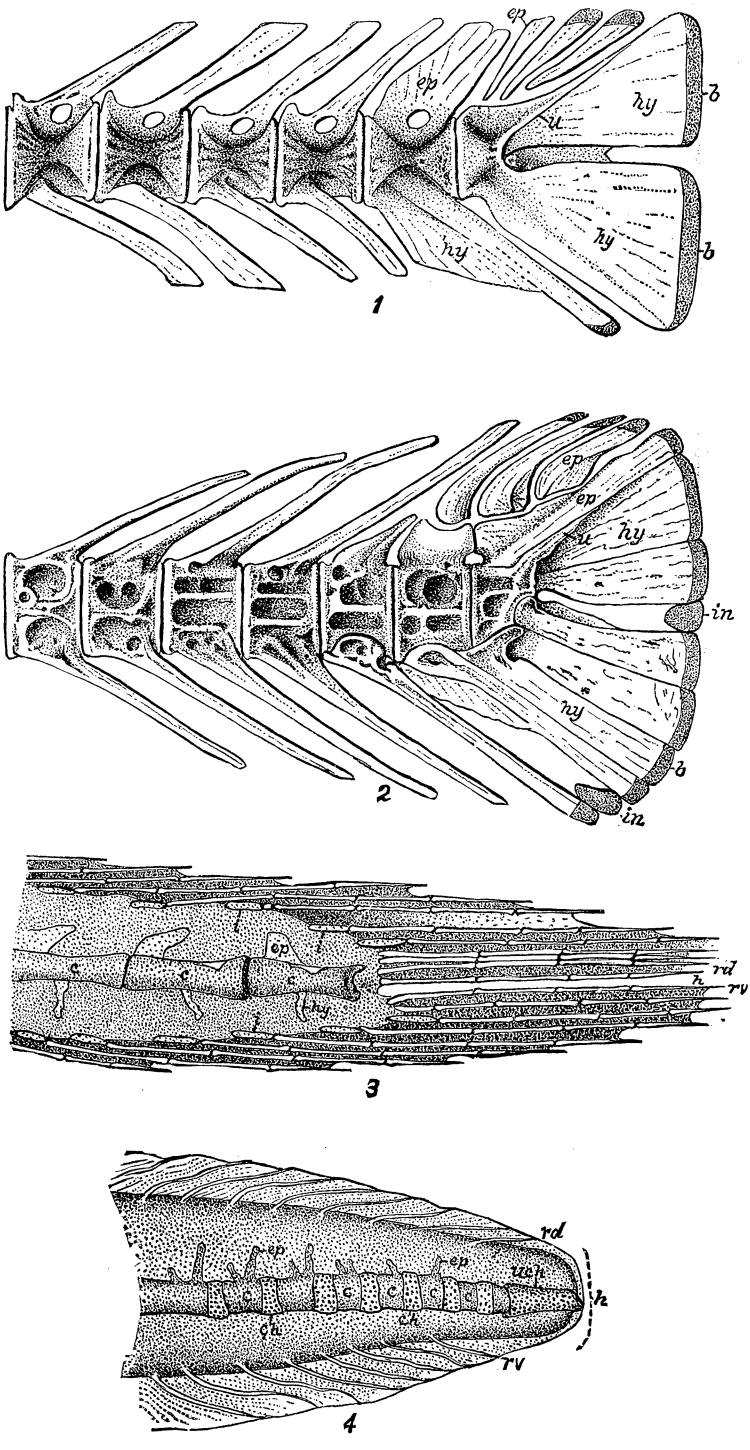
PLATE XIV.—Restoration of *Xenacanthus decheni*, an Ichthyotomous Elasmobranch from the Coal Measures of Alsace, much reduced. From Brongniart and Sauvage.

PLATE XV.—Fig. 1, *Chimæra monstrosa* L. ♂. Fig. reduced from Agassiz's Poissons Fossiles, showing opisthural filament. Fig. 2, Side view

of embryo ray in the lophocercal stage, natural size, from a specimen taken near Wood's Holl, Mass. Fig. 3, Lophocercal tail of young flounder 6 mm. long. Fig. 4, Lophocercal tail of young flounder a little older than the preceding, beginning to show a slight upbending of the notochord, and the first trace of the permanent caudal lobe (*pc*) and opisthural lobe (*op*). Fig. 5, Caudal lobe of a somewhat older flounder, showing indentation and definition of permanent fin-rays. Fig. 6, Specimen with tip of notochord still more reflexed than in the preceding; permanent caudal and opisthural lobes somewhat more distinct. Fig. 7, Permanent (*pc*) and opisthural lobes (*op*) now form a sharp angle where they join; distinction between permanent and embryonic rays well marked. Fig. 8, Permanent caudal as long as opisthural lobe (*op*). Fig. 9, Cartilaginous supports of fin-rays are now strongly developed; the end of the chorda has begun to degenerate and approximate the position which it will occupy permanently as the urostyle. Fig. 10, The caudal has become more rounded, the opisthure (*op*) is almost wholly absorbed, and the notochord has suffered atrophy somewhat, and now presents a still closer approximation to the form of the urostyle of the adult. Figs. 3–10 inclusive after A. Agassiz.

PLATE XVI.—Fig. 1, Caudal skeleton of Coccosteus after Pander; *ep* and *hy*, epural and hypural elements, all of which do not bear rays, but as in Pterichthys, extended out only so far as the scaly covering of the tail; *d*, dorsal; *a*, anal fins. Fig. 2, *Polypterus bichir*, caudal skeleton, from Agassiz's Poissons Fossiles, modified from Kölliker; *ep*, styliform ray-bearing and nodular non-ray-bearing interspinous epural elements; *ep*, neural spines; *hy*, hypural ray-bearing elements. Fig. 3, Lepidosteus, caudal skeleton from Kölliker, adult; showing urochord more prolonged and attenuated than in the preceding. Fig. 4, Platysomus restored, after Agassiz's Poissons Fossiles; *ep* and *hy* epural and hypural pieces; *u*, urochordal end of skeletal axis, which was mainly notochordal. Fig. 5. Lepidosteus, tail of young specimen 11 cm. long, from Balfour and Parker; *cd*, permanent caudal; *ff*, eradiate fin fold of opisthure; *op*, opisthure; *my my*, its myotomes. Fig. 6, Lepidosteus, young, 21 mm. long, side view; dissected and magnified so as to show its structure at this stage; *ep* and *hy*, epural and hypural cartilaginous rudiments of the neural and hæmal arches; *ch*, chorda; *cb*, its opisthural portion, which afterwards becomes partially aborted and included in the upper part of the tail; *cd*, tip of fold, which becomes the permanent caudal; *op*, opisthural lobe of the larval tail; *ff*, lophocercal fin-fold, which contains horn-fibres throughout its extent, *hf*. After Balfour and Parker. Fig. 7, Magnified view of the caudal skeleton of a young Cyprinodont, Gambusia, ⅓ of an inch long, and which was removed from the ovarian follicle in which it developed; *ch*, chorda dorsalis; *ep* and *hy*, epural and hypural cartilages; *ms*, medulla spinalis; *r r r*, rays. Fig. 8, *Centrina salviani*, caudal skeleton of adult; *ep* and *hv*, as before; *va*, ver-

PLATE XVIII.



Homocercal and Gephyrocercal Fins.

tebral axis; *fff*, its dorsal and ventral membranous lobes, which include numerous horny and partly osseous supporting fibres. From Günther.

PLATE XVII.—Fig. 1, *Salmo fario*, adult, caudal skeleton; *b* and *bi*, basilar cartilages; *ep*, epural, and *hy*, hypural elements; *m*, lateral membrane bone, which has had an epural cartilaginous element as its nucleus; *in*, intercalary cartilage; *u*, urostyle; *op*, opisthure. After Lotz. Fig 2, *Salmo salar*, adult, caudal skeleton; lettering as in Fig. 1. From Lotz. Fig. 3, *Barbus fluviatilis*, adult, caudal skeleton; lettering as before. From Lotz.

PLATE XVIII.—Fig. 1, *Cottus gobio*, adult, caudal skeleton; lettering as in Plate XVI. From Lotz. Fig. 2, *Perca fluviatilis*, adult, caudal skeleton; lettering as before. From Lotz. Fig. 3, *Echiodon dentatus*, adult, gephyrocercal caudal extremity; *c*, centra; *ep* and *hy*, hypural processes; *b*, basilar cartilages: *i*, interspinous cartilages; *h*, hiatus between dorsal rays (*rd*) and postanal rays (*rv*); x 17. From Emery. Fig. 4, *Fierasfer acus*, gephyrocercal caudal extremity; *ep*, epural processes; *c c c*, centra not in contact; *ch ch ch*, membranous or cartilaginous central intervals; *uch*, exserted end of chorda, or urochord; *h*, hiatus between last dorsal rays (*rd*) and last postanal rays (*rv*); x 55. From Emery.

A ZOÖLOGICAL RECONNOISSANCE IN GRAND MANAN.

BY J. WALTER FEWKES.

ON the side towards Eastport, Grand Manan presents a series of lofty cliffs rising abruptly out of the sea, so precipitously that it would be almost impossible to climb from the shore to their summits. Only in a few places is this rampart broken through, leaving sheltered coves where boats can find anchorage. Ordinarily the lofty cliffs rise abruptly from the sea, and the few stretches of beach crowded in between the foot of the cliff and the water are exceptional, and limited in extent. Deep into this lofty buttress of rock there extends at one point on this side of the island a deep fiord, known as Dark Harbor, so-called because in former times its heights were covered with sombre trees. The